PROGAMOTAENIA NYBELIN (CESTODA: ANOPLOCEPHALIDAE): NEW SPECIES, REDESCRIPTIONS AND NEW HOST RECORDS

by I. BEVERIDGE*

Summary

BEVERIDGE, I. (1980) *Progamotaenia* Nybelin (Cestoda: Anoplocephalidae): new species, redescriptions and new host records. *Trans. R. Soc. S. Aust.* **104**(4), 67-79, 30 May, 1980.

The following species are described: *Progamotaenia spearei* sp. nov., from *Thylogale stigmatica*, distinguished by its small size, in having paired uteri, a fringed velum and testes in two groups, and *Progamotaenia johnsoni* sp. nov. from *Lagorchestis conspicillatus*, which has an external seminal vesicle covered with glandular cells and testes distributed in two elongate groups. *P. bancrofti* (Johnston) and *P. diaphana* (Zschokke) are redescribed, and *Lasiorhinus latifrons* is considered to be the usual host of the latter species. *P. zschokkei* (Janicki) is reported for the first time from *Macropus agilis*, *Onychogalea fraenata* and *O. unguifera*; additional records of this species from *Petrogale penicillata*, *Lagorchestes conspicillatus* and *Thylogale stigmatica* are given.

Introduction

Although the anoplocephalid cestodes of Australian marsupials have been the subject of a recent review (Beveridge 1976), continued collecting has resulted in the discovery of additional new species of *Progamotaenia* (Beveridge 1978, Beveridge & Thompson 1979). To date most collections have been from marsupial species inhabiting the south-eastern part of the continent. Recent collecting from macropodids in north Queensland has led to the discovery of two new species of *Progamotaenia*.

Progamotaenia bancrofti and *P. diaphana*, were recently redescribed by Beveridge (1976) on the basis of very limited or poorly preserved material only. Both are well represented in recent collections, and the opportunity is taken here to describe them fully.

Materials and methods

Cestodes collected from the small intestines of macropodids were washed in tap water, relaxed in water for several hours and fixed in 10% formalin or Serra's fluid. They were stained with Celestine blue, cleared in methyl salicylate or clove oil and mounted in balsam. Hand cut transverse sections and serial histological sections cut in transverse and longitudinal planes were prepared. Drawings were made with the aid of a camera lucida. Measurements are given in mm as the range followed by the mean of five measurements (where available) in parenthesis.

Type specimens have been deposited in the South Australian Museum (SAM).

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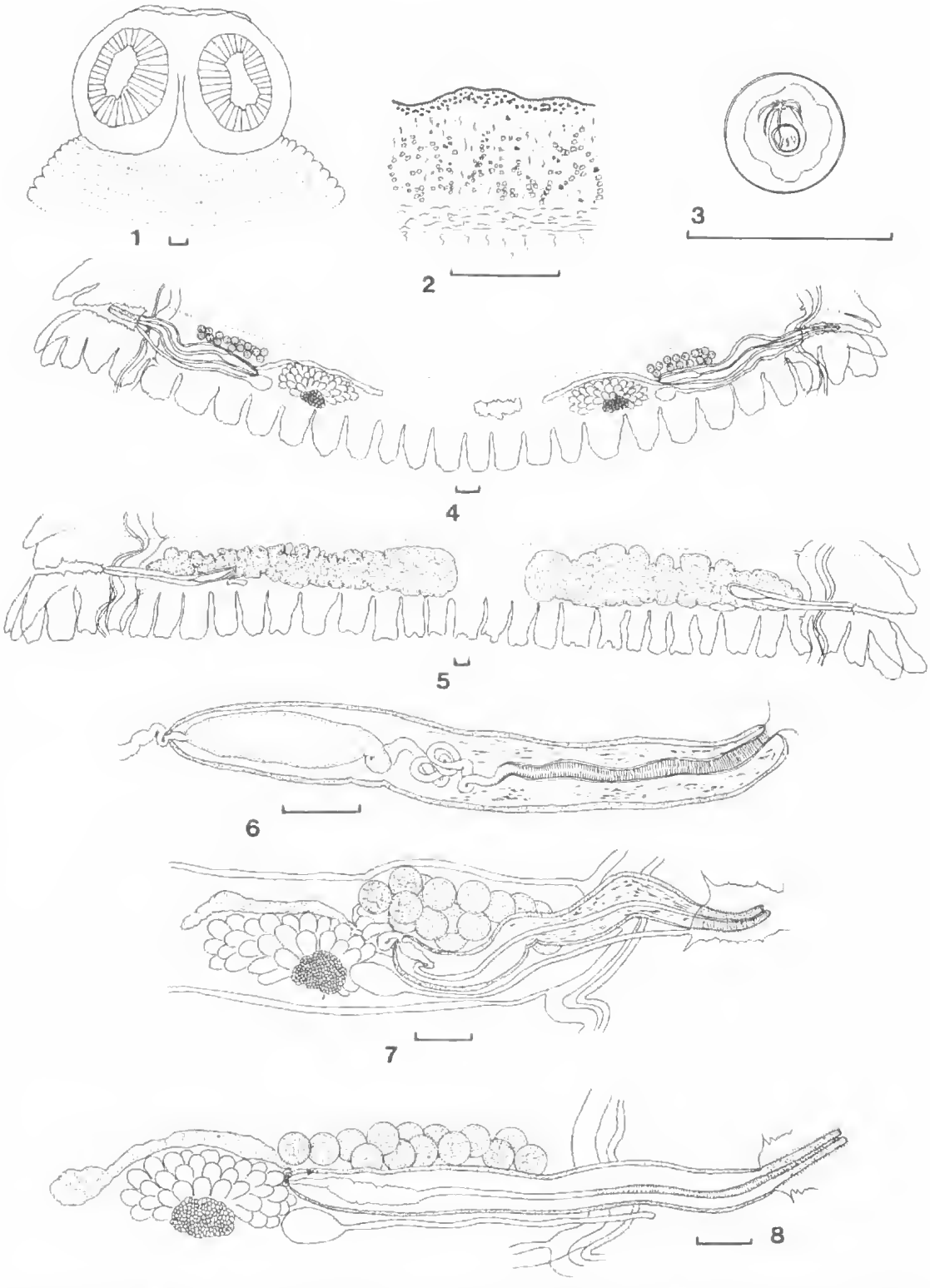
Progamotaenia spearei sp. nov.

FIGS 1–8

Types: holotype (slide) from small intestine of *Thylogale stigmatica* Gould 1860, Tolga Queensland, 16 x. 1978, collected by I. Beveridge, in SAM V1920; 4 paratype slides, same data V1921–V1924; 1 paratype, spirit material and serial sections V1925, V1926.

Description: Length 26–30 (28); width 5–7 (6); scolex diameter 1.31–1.52 (1.44); sucker diameter 0.56–0.74 (0.67) x 0.47–0.58 (0.55); neck 0–0.21 (0.09); no. proglottides 71–85 (78); mature proglottides 3.8–4.0 (3.9) x 0.21–0.28 (0.23); gravid proglottides 4.1–5.8 (5.4) x 0.56–0.74 (0.65); cirrus sac in mature proglottides 0.60–0.92 (0.81) x 0.08–0.12 (0.10); cirrus sac in gravid proglottides 0.93–0.98 (0.94) x 0.11–0.14 (0.12); no. testes per proglottis 30–40 (34); testis diameter 0.06–0.09 (0.08); ovary 0.50–0.56 (0.53) x 0.18–0.21 (0.20); vitellarium 0.11–0.18 (0.15) x 0.08–0.12 (0.10); dorsal osmoregulatory canal 0.02–0.03 (0.02); ventral osmoregulatory canal 0.03–0.09 (0.07); egg 0.06–0.08 (0.07); pyriform apparatus 0.03-0.04 (0.04); oncosphere 0.02.

Short broad tapeworms with relatively few proglottides. Scolex squat, almost globose, prominently four-lobed, each lobe with muscular, cup shaped sucker. Neck absent or, if present, very short, segmentation beginning very close to suckers. Proglottides extended transversely, craspedote with broad, fringed velum consisting of about 25–35 tongue shaped projections which are frequently folded and overhand 1/2–2/3 of the adjacent proglottis. Mature proglottides with approximate length:



Figs 1-8. *Progamotaenia spearei* sp. nov. 1. scolex; 2. transverse histological section through cortex showing musculature; 3. egg; 4. mature proglottis; 5. gravid proglottis; 6. cirrus sac; 7. lateral region of mature proglottis prior to vaginal atrophy and uterine filling; 8. lateral region of mature proglottis at commencement of uterine filling, showing atrophy of vagina. Scale lines 0.1 mm.

width ratio of 1:14 to 1:20. Gravid proglottides with ratio 1:6 to 1:10. Cortex thick. longitudinal muscles developed, numerous, not arranged in regular bundles, denser towards cortico-medullary junction. Transverse muscles well developed, forming thick band running along cortico-medullary junction. Dorso-ventral muscles prominent, crossing cortex and medulla at irregular intervals. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Two transverse canals connect left and right osmoregulatory canals at posterior margin of each proglottis. Canal connecting ventral vessels of moderate size, readily observed; canal connecting dorsal canals extremely fine, seen only with difficulty. Fine accessory canals associated with ventral canal in some proglottides; accessory canals branch and anastomose irregularly. Junction of osmoregulatory canals in scolex not seen. Genital ducts cross osmoregulatory canals dorsally. Genital atrium prominent, very long; walls lined with thickened tegument, opening in middle of lateral proglottis margin. Cirrus sac elongate, musculature of walls strongly developed, crossing beyond osmoregulatory canals, reaching almost to ovary. Cirrus narrow, distal third covered with numerous prominent spines; mid-third unarmed, greatly coiled when retracted, uncoiled when cirrus is everted. Internal seminal vesicle prominent, elongate. External seminal vesicle absent. Vas deferens coils anteriorly and medially from cirrus sac. Vasa efferentia not seen. Testes distributed in two compact clusters anterior to cirrus sac, extending medially from osmoregulatory canals to poral side of ovary; never extending medially beyond ovary to form single band. Vagina tube-like, opening to genital atrium posterior to cirrus sac. Vagina leads medially to diminutive, ovoid, seminal receptacle situated posterior to median pole of cirrus sac, lateral to ovary. Ovary fan-shaped, composed of numerous clavate lobules, on ventral aspect of medulla. Vitellarium ovoid, situated posterior and dorsal to ovary. Mehlis' gland spherical, medial to vitellarium. Uterus transverse, tube-like, paired in each proglottis, anterior to ovary. Fully developed uterus sacciform with prominent anterior diverticula; posterior diverticula very small. Uteri fill space between osmoregulatory canals but do not extend beyond canals except in last few gravid proglottides; uteri cross canals dorsally but do not reach posterolateral corners of proglottis. Egg spherical, thick-shelled. Pyriform apparatus conical, terminating in reflexed filaments. Genital primordia appear in 6–10th proglottis; genital organs are developed by 15–18th proglottis; sperm present in internal seminal vesicle in 15–20th proglottis; filling of seminal receptacle and atrophy of vagina occur in 16–24th proglottis; uterus begins to fill in 22–26th proglottis; eggs fully formed in 69–73rd proglottis.

Vestigial supernumerary vitellaria, ovaries or uterine fragments present in proglottides of some strobilae, of variable size, arranged between two normal sets of genital organs.

Discussion: *Progamotaenia spearei* most closely resembles *P. proterogyna* (Fuhrmann 1932) in external features, being a small worm, with few proglottides and with a fringed velum. It differs in the shape of fringes of the velum, the occurrence of testes in two distinct groups rather than in a continuous band and in the occurrence of vaginal atrophy following insemination. *P. gynandrolinearis* Beveridge & Thompson 1979 is another small species, but the velum is not fringed. *P. spearei* resembles *P. lagorchestis* (Lewis 1914) and *P. thylogale* Beveridge & Thompson 1979 in having a fringed velum, paired uteri and testes occurring in two lateral groups, but differs from both species in its small size, small number of proglottides, the rapidity of development of the genital organs in the strobila and the small number of testes.

This species is named after Dr R. Speare, James Cook University of North Queensland, in appreciation of help given in collecting material.

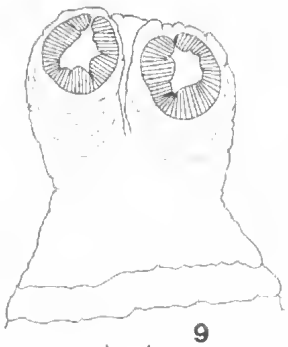
Progamotaenia johnsoni sp. nov.

FIGS 9–15

Types: holotype (without scolex) from small intestine of *Lagorchestes conspicillatus* Gould, 1842, Mingela, Queensland, 10.v.1979, collected by I. Beveridge, 6 slides, spirit material and serial section in SAM V1918; paratype slide, same data, V1919.

Material examined: from *Lagorchestes conspicillatus*: types; 4 specimens (non gravid), Inkerman Station, Qld, 7.ix.1977, P. M. Johnson.

Description: Length 178 (holotype); width 13 (holotype); scolex diameter 0.74–1.21 (0.86); sucker diameter 0.30–0.42 (0.32) x 0.28–0.36



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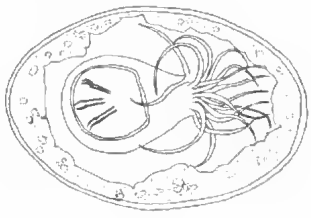

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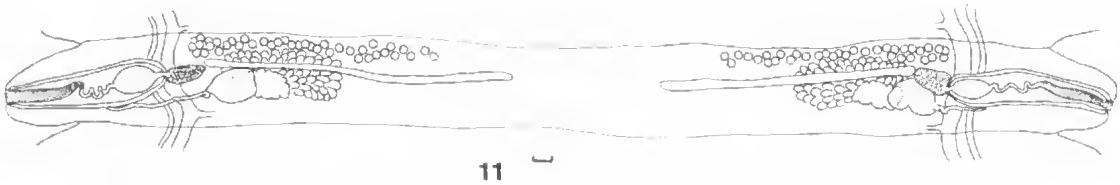

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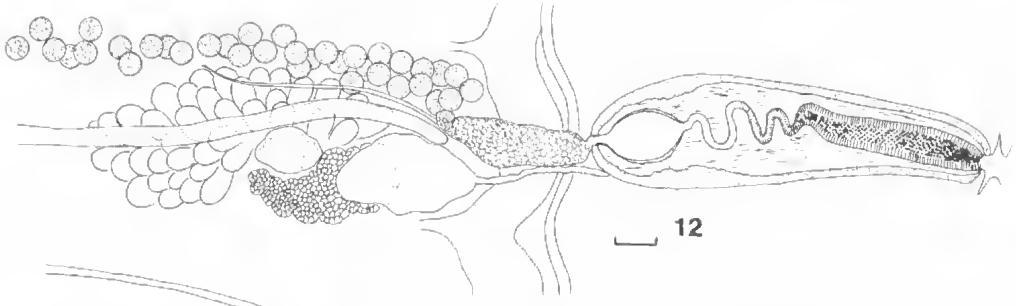

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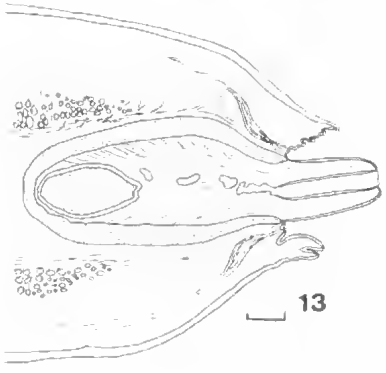

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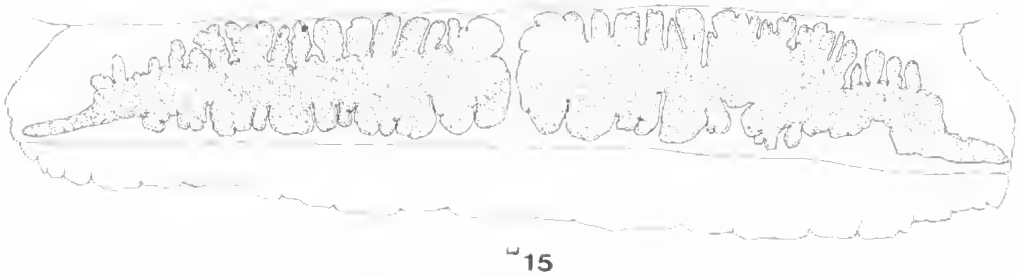

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(0.31); neck 0.16–0.36 (0.26); no. proglottides 272 (holotype); mature proglottides 5.4–7.0 (6.2) x 0.52–0.56 (0.54); gravid proglottides 9.4–9.8 (9.6) x 0.92–0.99 (0.96); cirrus sac in mature proglottides 0.46–1.31 (0.90) x 0.16–0.29 (0.25); in gravid proglottides 1.08–1.18 (1.14) x 0.34–0.36 (0.35); no. testes per proglottis 100–190 (178); testis diameter 0.05–0.08 (0.06), ovary 0.62–0.80 (0.72) x 0.34–0.38 (0.36); vitellarium 0.30–0.40 (0.37) x 0.17–0.23 (0.18); Mehlis' gland 0.10–0.14 (0.12); dorsal osmoregulatory canal 0.02–0.04 (0.03); ventral osmoregulatory canal 0.08–0.29 (0.18); egg 0.064–0.072 (0.068); pyriform apparatus 0.024–0.28 (0.025); oncosphere 0.009–0.016 (0.015).

Large, broad, ribbon-like worms. Scolex broad, four-lobed, with cup-shaped sucker at apex of each lobe. Suckers with anterior margins cleft. Neck short. Proglottides greatly extended transversely, craspedote, with broad, fleshy, folded velum covering much of adjacent proglottis. Mature proglottides with approximate length:width ratio of 1:10 to 1:13. Gravid proglottides with ratio of 1:9 to 1:11. Longitudinal musculature powerfully developed, composed of pallisades of muscle bundles. Bundles circular or oval in section; outer bundles smaller, with fewer fibres. Outer longitudinal musculature consists of ring of individual fibres, immediately external to muscle bundles. Transverse muscles well developed, forming broad band immediately internal to longitudinal muscle bundles. Few, scattered transverse muscle fibres present in outer cortex. Towards lateral margins of proglottides, transverse muscles from cortex and cortico-medullary junction fuse into thick band of muscle encircling cirrus sac and extending to genital atrium. Dorso-ventral muscle fibres well developed, prominent, crossing cortex and medulla at regular intervals. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Scolex osmoregulatory canals not seen. Genital ducts cross osmoregulatory canals dorsally. Genital atrium shallow, with corrugated walls, opening in middle of lateral proglottis margin. Cirrus sac powerfully developed, with thick muscular walls, extending to medial margin of, or beyond longitudinal osmoregulatory canals into medulla. Cirrus wide at distal extremity, heavily armed with spines; mid-region of narrower diameter, distal part armed, proximal part unarmed. Internal seminal vesicle ovoid, with thick, muscular walls. External seminal vesicle large, elongate, sometimes coiled, covered externally with layers of glandular cells. Vas deferens leads medially from external seminal vesicle, gradually diminishing in diameter. Vasa efferentia not seen. Testes in two lateral groups anterior to female genitalia, each group extending from osmoregulatory canals medially beyond medial border of ovary, occasionally almost to middle of proglottis. Testes in 2–4 longitudinal and 1–3 transverse rows. Vagina tube-like, narrow, opening to genital atrium posterior to cirrus sac. Vagina leads medially, along posterior border of cirrus sac to ovoid seminal receptacle situated lateral to vitellarium. Ovary fan-shaped, composed of numerous clavate lobules, on ventral aspect of medulla. Vitellarium ovoid to reniform, dorsal and posterior to ovary. Mehlis' gland spherical, anterior to vitellarium. Uterus transverse, tube-like, paired in each proglottis, dorsal to ovary. Tubular uterus extends from near centre of proglottis, dorsal to ovary, anterior to vitellarium, terminating between proximal pole of external seminal vesicle and seminal receptacle. Fully developed uterus sacciform, with prominent anterior and posterior diverticula. Uteri cross longitudinal osmoregulatory canals dorsally, extending to postero-lateral corners of proglottis. Egg ellipsoidal, thick shelled. Pyriform apparatus conical, terminating in reflexed filaments. Genital primordia appear in c.20th proglottis; cirrus sac developed by 26–30th proglottis; internal seminal vesicle fills with sperm in 33–47th proglottis; insemination occurs in 40–46th proglottis; vaginal atrophy not seen; full maturity of female genitalia reached in c.50th proglottis.

Discussion: Although described from a limited amount of material, *Progamotaenia johnsoni* is sufficiently distinctive to be readily recognised. The gravid holotype is, unfortunately,

Figs 9-15. *Progamotaenia johnsoni* sp. nov. 9, scolex; 10, egg; 11, mature proglottis; 12, lateral region of mature proglottis showing genitalia; 13, transverse histological section through lateral region of mature proglottis showing cirrus sac and musculature; 14, transverse histological section through cortex showing musculature; 15, gravid proglottis. Scale lines, fig. 10, 0.01 mm, figs 9, 11–15, 0.1 mm.

without scolex, but the remaining specimens are not gravid. Mature proglottides of the specimens from Inkerman are identical morphologically with those of the holotype, and there is no doubt that they are conspecific. There is no possibility of confusion with congeners that occur in *L. conspicillatus*, reviewed by Beveridge & Thompson (1979), since other intestinal species occurring in this host in eastern Australia have markedly fimbriated vela (Beveridge 1976).

P. johnsoni most closely resembles *P. bancrofti* in being a very large, thick species with greatly extended proglottides, a broad unfringed velum, a powerfully developed cirrus sac and armed cirrus and an external seminal vesicle covered with glandular cells. The last characteristic distinguishes *P. johnsoni* and *P. bancrofti* from all congeners. *P. johnsoni* is distinguished from *P. bancrofti* by a smaller scolex, a muscular wall to the internal seminal receptacle, the presence of a pyriform apparatus in the egg, and most importantly of all, in the distribution of the testes, which in *P. johnsoni* extend from the osmoregulatory canals beyond the medial margin of the ovary almost to the centre of the proglottis, but which are restricted in *P. bancrofti* to the region lateral to the ovary. Although in every proglottis of *P. johnsoni* examined, the testes were distributed in two groups, in some cases, the distance between the two groups of testes in the centre of the proglottis was quite small and examination of further specimens may well reveal instances in which the two groups of testes fuse in the midline.

An unusual feature of the anatomy of *P. johnsoni* is the condensation of muscle fibres to form a sphincter-like annulus around the distal extremity of the cirrus sac. A sphincter surrounding the genital atrium has been described in a number of species of *Progamotaenia* (Baer 1927, Lewis 1914), but Beveridge (1976) considered that the structures reported by the earlier writers in no way constituted a sphincter, consisting as they did of an accumulation of parenchymatous elements. The structure described above in *P. johnsoni* is a distinctive muscular structure which is in some respects sphincter-like. However, its function is not known at present.

The species is named after Mr P. M. Johnson, National Parks and Wildlife Service, Pallarenda, Queensland, in appreciation of help given in collecting specimens.

Progamotaenia bancrofti (Johnston, 1912)

FIGS 16–23

Material examined: from *Onychogalea fraenata*: 2 specimens, Dingo, Qld, 12.vii.1975, J. E. Nelson; 1 specimen, Dingo, Qld., (captive animal) March, 1978, I. Beveridge.

From *Onychogalea unguifera*: 6 specimens, Wernadinga Station via Burketown, Qld, 6.viii.1979, R. Speare and P. M. Johnson; 8 specimens, Chadshunt Station via Mt Surprise, Qld, 7.viii.1979, R. Speare and P. M. Johnson; 2 specimens, 'Kimberley Ranges', W.A., 31.viii.1976, L. Keller.

Description: Length 198–312 (243); width 9–18 (14); scolex diameter 2.21–2.75 (2.46); sucker diameter 1.05–1.38 (1.25) x 0.88–1.28 (1.02); no. proglottides 643–672 (660); mature proglottides 6.6–9.5 (7.9) x 0.34–0.42 (0.38); gravid proglottides 9.2–10.6 (9.8) x 0.40–0.70 (0.55); cirrus sac in mature proglottides 0.66–1.52 (1.11) x 0.23–0.34 (0.26); cirrus sac in gravid proglottides 1.4–1.9 (1.6) x 0.26–0.32 (0.29); no. testes per proglottis c. 200; testis diameter 0.06–0.09 (0.07); ovary 0.60–0.80 (0.67) x 0.24–0.35 (0.29); vitellarium 0.40–0.57 (0.47) x 0.14–0.24 (0.18); Mehlis' gland 0.11–0.17 (0.14); dorsal osmoregulatory canal 0.02–0.06 (0.04); ventral osmoregulatory canal 0.22–0.35 (0.30); egg 0.036–0.041 (0.039); embryophore 0.017–0.024 (0.018); oncosphere 0.014–0.020 (0.016).

Large, broad, ribbon like worms. Scolex large, globular, distinctly demarcated from scolex. Four cup-shaped suckers embedded within scolex. Neck absent. Proglottides greatly extended transversely, craspedote, with broad, fleshy, folded velum radiating outwards from strobila, covering ½ to ¾ of the adjacent proglottis. Mature proglottides with approximate length: width ratio of 1:20 to 1:23. Gravid proglottides with ratio 1:16 to 1:20. Terminal proglottides narrower with ratio 1:8.

Figs 16-23. *Progamotaenia bancrofti* (Johnston). 16. scolex; 17. transverse histological section through cortex showing musculature; 18, 19. eggs showing variation in shape and in thickness of embryophore; 20. lateral region of mature proglottis; 21. female genital complex, from hand cut transverse section; ventral towards top of page; 22. postmature proglottis showing tubular uterus; 23. gravid proglottis. Scale lines, figs 16, 23, 1.0 mm, figs 18, 19, 0.01 mm, figs 17, 20-22, 0.1 mm.

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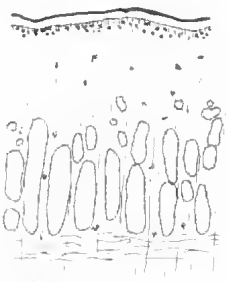

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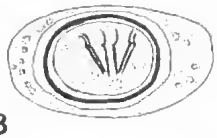

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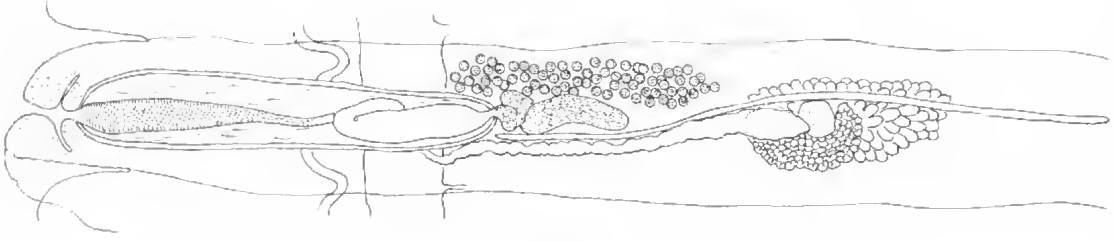

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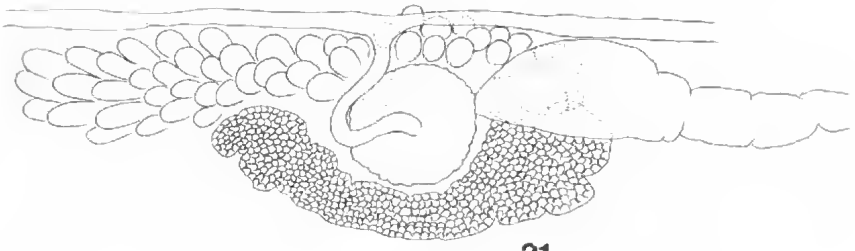

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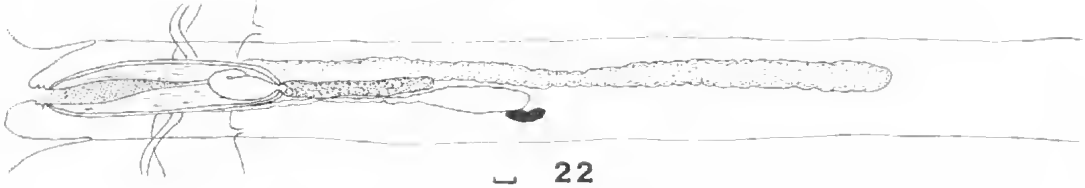

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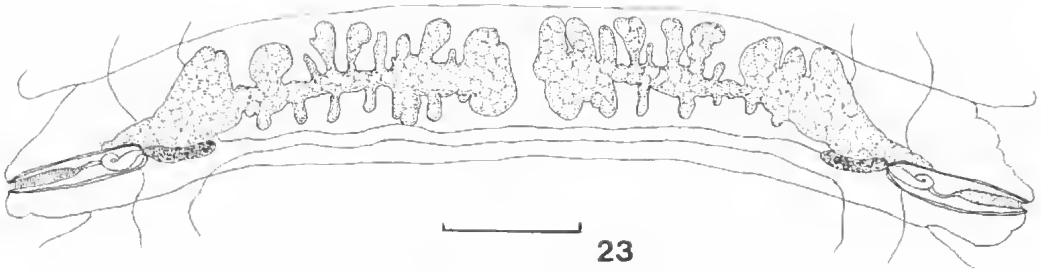

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Longitudinal musculature powerfully developed, composed of pallisades of muscle bundles. Bundles elongate, arranged radially, bundles towards periphery smaller, with fewer fibres. Transverse muscles well developed, forming a dense band along cortico-medullary junction. Dorso-ventral fibres prominent, crossing cortex and medulla at regular intervals. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Small accessory canal associated with ventral canal, on ventral side of ventral canal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Complex of very fine branching and anastomosing vessels associated with dorsal system at posterior margins of proglottides. In scolex, vessels lead to connecting ring vessel in transverse plane at level of anterior margins of suckers. Genital ducts cross osmoregulatory canals dorsally. Genital atrium shallow, with corrugated walls, opening in middle of lateral proglottis margin, causing interruption of velum. Cirrus sac powerfully developed with thick muscular walls, extends beyond osmoregulatory vessels into medulla. Cirrus widest at distal extremity, heavily armed with spines; mid-region coiled, unarmed. Internal seminal vesicle present, usually reflexed distally when filled. External seminal vesicle large, elongate, covered externally with layers of glandular cells. Vas deferens inconspicuous, coils anteriorly to testes. Vasa efferentia not seen. Testes distributed in two compact groups anterior to cirrus sac, extending from longitudinal osmoregulatory canals to lateral margin of ovary. Testes in 3–5 longitudinal and 4–6 transverse rows. Number of testes in each group could not be counted accurately.

Vagina tube-like opening to genital atrium posterior to cirrus sac, distal vagina seen only in serial sections. Vagina leads medially along ventral aspect of cirrus sac, crosses to dorsal aspect of medulla, gradually increasing in diameter. Seminal receptacle not clearly separated from vagina, situated lateral to vitellarium. Ovary fan shaped, composed of numerous clavate lobules, on ventral aspect of medulla. Vitellarium reniform, dorsal and posterior to ovary, partially enclosing Mehlis' gland, which is spherical, anterior to vitellarium.

Uterus transverse, tube-like, paired in each proglottis, dorsal to ovary. Tubular uterus extends from near proglottis midline, anterior to vitellarium and dorsal to ovary, runs along ventral aspect of medulla almost to longitudinal osmoregulatory canals. Fully developed uterus sacciform, with prominent anterior diverticula, and fewer, smaller posterior diverticula; crossing longitudinal osmoregulatory canals dorsally, extending to posterolateral corners of proglottides. Egg elongate ovoid, outer wall thin. Pyriform apparatus absent, even in eggs from faeces; embryophore surrounding egg thick, ellipsoidal.

First mature proglottis 165–235th; filling of seminal receptacle occurs at approximately same time as sperm appears in internal seminal vesicle; vagina does not atrophy following insemination; uterine filling commences in c. 300th proglottis.

Discussion: The descriptions of *Progamotaenia bancrofti* by Johnston (1912), Nybelin (1917) and Beveridge (1976), are unsatisfactory because only a limited number of specimens was available. The original description by Johnston (1912) was based on a single non-gravid specimen from *Onychogalea fraenata*, the description by Nybelin (1917) was based on four specimens from *O. unguifera*, all of which were severely contracted, and only one was gravid. Beveridge (1976) re-examined all these specimens but was able to add little. The type host, *O. fraenata* is now almost extinct, so that the main source of material for the present redescription came from the related wallaby, *O. unguifera*.

Although ample material was available, the species is extremely difficult to examine because of its large size and the thickness of the longitudinal musculature and velum. Nevertheless, the present re-description supports earlier descriptions in most respects, differing only in the features of the uterus and external seminal vesicle. The uterus commences development as a transverse tube, gradually enlarging in diameter as it fills with eggs. In postmature proglottides, in which the ovary has involuted, the uterus remains tube-like, with little evidence of anterior and posterior diverticula. The latter develop subsequently in gravid proglottides. The lack of diverticula on the uteri of the holotype described by Beveridge (1976), presumably reflects the immaturity of the specimen rather than a significant difference between it and the new material.

A prostate at the proximal pole of the cirrus sac was described in *P. bancrofti* by Nybelin (1917) and Beveridge (1976). The structure

is in fact an external seminal vesicle, differing from comparable structures in congeners in being elongate rather than ovoid, and surrounded by a mass of glandular cells. This latter feature serves to separate *P. bancrofti* from all congeners except *P. johnsoni*. However, here the term "prostate" has been discarded in favour of "external seminal vesicle" to avoid confusion with a structure (also termed the prostate) described in certain species of the anoplocephalid genera *Andrya* Railliet 1893 and *Diandrya* Darrah 1930. Rausch (1976) has cast considerable doubt on the existence of a prostate in these genera, suggesting that the organ in question is the external seminal vesicle.

Nybelin (1917) stated that a pyriform apparatus was not present, but Beveridge (1976) cautioned that the few specimens available to Nybelin may not have been fully gravid. In the new material, a pyriform apparatus was found neither in the terminal proglottides of strobilae which were fully gravid, nor in shed proglottides collected from the large intestine of the host. It was not established whether a pyriform apparatus develops in the external environment following voiding. The only congener in which a pyriform apparatus is lacking is *P. lagorchestis*. In both species the egg is elongate rather than spherical or ovoid.

Serial longitudinal sections of the strobila revealed that the distal vagina is an extremely narrow duct, but that it remains patent even in proglottides in which the uterus is in the process of filling. The distal vagina was not seen in every proglottis, but in a sufficient number to indicate that earlier descriptions have been incorrect, and that the distal vagina is merely difficult to find, even in sections, rather than having atrophied following insemination.

Further collecting has confirmed *Onychogalea fraenata* and *O. unguifera* as hosts of *P. bancrofti*. The species has not been found in *Wallabia bicolor* or *Setonix brachyurus* apart from a single report by Sandars (1957). Her brief descriptions do not conform to earlier more detailed descriptions (Beveridge 1976). The location of Sandars' specimens is unknown, and their identifications may be in error.

P. bancrofti was present in seven of ten *O. unguifera*, with either one or two cestodes per wallaby. The cestodes occurred in the ileum.

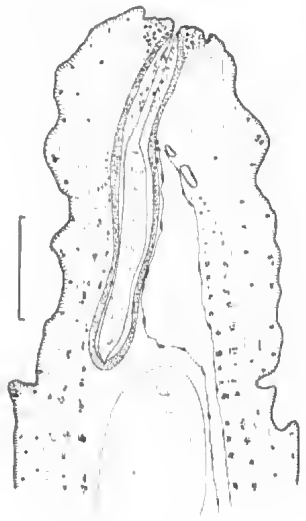
Progamotaenia diaphana (Zschokke, 1907)
FIGS 24–29

Material examined: types from *Lasiorhinus latifrons*; numerous fragmented specimens, from bile ducts, Swan Reach, S.A., 12.v.1977, I. Beveridge; 14.ix.1978, M. Gaughwin.

Description: Length up to 102; width to 2; scolex diameter 0.32–0.46 (0.38); sucker diameter 0.13–0.16 (0.15); neck 0.07–0.16 (0.11); mature proglottides 1.1–1.9 (1.5) x 0.23–0.43 (0.31); gravid proglottides 1.7–2.6 (2.0) x 0.28–0.35 (0.34); cirrus sac in mature proglottides 0.17–0.39 (0.29) x 0.06–0.09 (0.07); cirrus sac in gravid proglottides 0.22–0.33 (0.28) x 0.04–0.09 (0.07); no. testes per proglottis 39–64 (51); testis diameter 0.04–0.05 (0.04); ovary 0.08–0.14 (0.11) x 0.04–0.10 (0.08); vitellarium 0.06–0.08 (0.07) x 0.04–0.06 (0.05); Mehlis' gland 0.04–0.05 (0.05); dorsal osmoregulatory canal 0.01–0.02 (0.02); ventral osmoregulatory canal 0.02-0.04 (0.03); egg 0.07–0.08 (0.08); pyriform apparatus 0.04–0.05; oncosphere 0.03.

Small, fragile worms, almost transparent and easily broken when fresh. Scolex prominently four lobed, with each muscular, cup shaped sucker borne on arm like extentions of scolex. Scolex frequently, but not invariably dark, pigmented. Pigment distributed mainly on arms and at apex of scolex, as masses of small, brown staining accumulations of granules in the cortex immediately below the tegument. Small pigmented granules scattered around vicinity of central nervous system. Neck present in relaxed specimens. Proglottides extended transversely, craspedote, with narrow (c. 0.05) straight-edged velum overhanging adjacent proglottis. Mature proglottides with approximate length: width ratio of 1:2.5 to 1:8. Gravid proglottides with ratio 1:5.5 to 1:7.5. Longitudinal muscles poorly developed, composed of 2 rings of fibre bundles with 2 to 8 fibres per bundle. Transverse muscle consists of individual fibres running along cortico-medullary junction. Dorso-ventral muscle fibres single, crossing cortex and medulla at irregular intervals.

Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Two transverse canals connect left and right osmoregulatory canals at posterior margin of each proglottis. Canal connecting ventral vessels of moderate size, readily observed; canal connecting dorsal vessels minute, seen only with difficulty, function



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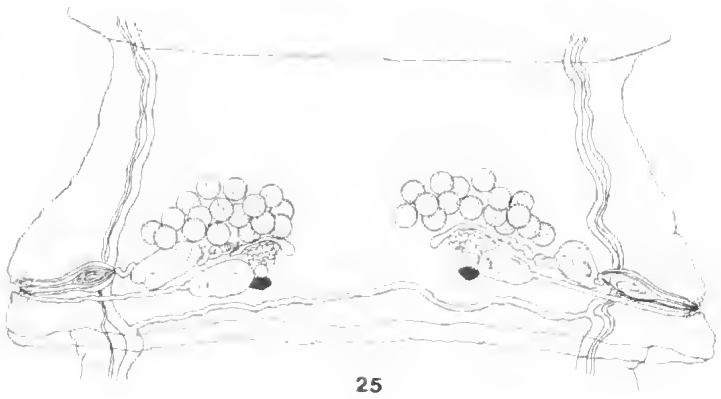

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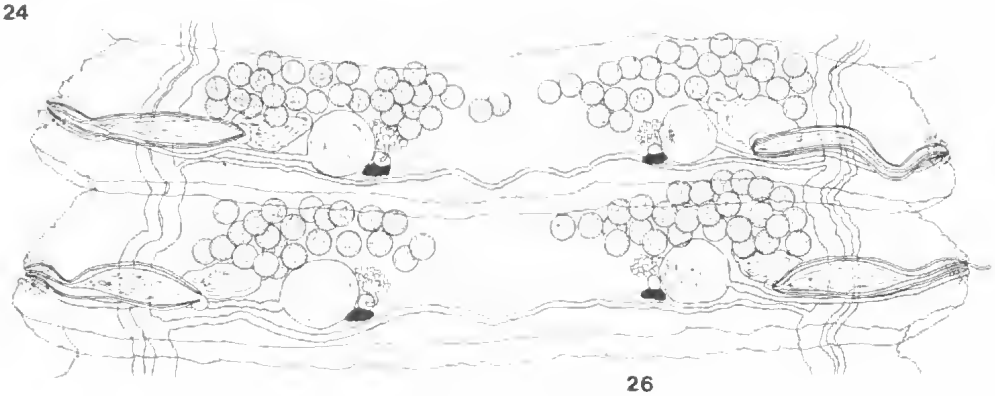

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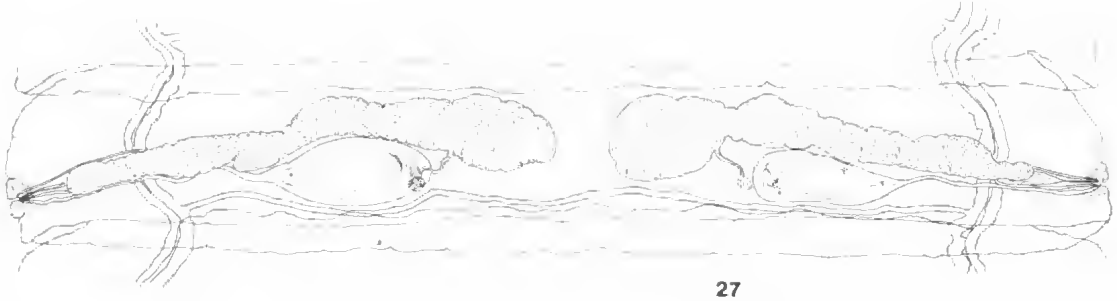

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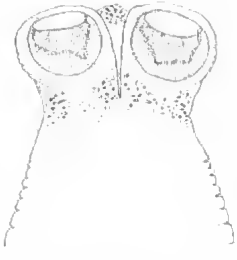

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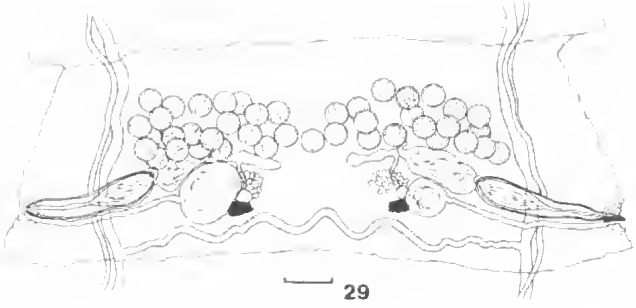

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of osmoregulatory canals in scolex not seen. Genital ducts cross osmoregulatory canals dorsally. Genital atrium of insignificant size, sometimes situated on small genital papilla. Atrium in posterior part of lateral proglottis margin, dividing margin in ratio of 1:2 to 1:3. Cirrus sac narrow, clavate, musculature of walls weakly developed, always reaching and usually extending beyond longitudinal osmoregulatory canals. Cirrus narrow, uncoiled, armed with minute spines, only clearly visible on exerted cirri. Prominent internal seminal vesicle present. External seminal vesicle large, ovoid, extending to lateral margin of, or occasionally anterior to, seminal receptacle. Vas deferens coiled, passes anteriorly, diminishing in diameter. Vasa efferentia not seen. Testes distributed between lateral osmoregulatory canals anterior to female genitalia. Testes either in two groups extending from longitudinal canals to medial side of female genitalia, or in continuous band across proglottis, with testes more numerous in lateral parts of band. Both forms of testis arrangement occur together in some strobilae. Vagina tube-like, opening to genital atrium posterior to cirrus sac. Vagina leads medially to large ovoid, thin-walled seminal receptacle. Ovary fan-shaped, composed of numerous, clavate lobules, on ventral aspect of medulla. Vitellarium ovoid or reniform, posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium, dorsal to ovary. Uterus transverse, tube-like, paired in each proglottis, anterior to seminal receptacle and ovary. Fully developed uterus sacciform, without diverticula, crossing longitudinal osmoregulatory canals dorsally and reaching postero-lateral corner of proglottis. Uteri of proglottis may fuse in mid-line on rare occasions. Egg spherical, thick-shelled. Pyriform apparatus either conical or terminating in two horns, numerous reflexed filaments attached to apex of pyriform apparatus.

Sperm first appears in external and internal seminal vesicles in c.105th proglottis; seminal receptacle fills with sperm in c.110th proglottis, after male system commences to function. Vagina does not atrophy following insemination. Ovary fully developed from c.140th to 150th proglottis, involutes over 2–3 proglottides. Uterus begins to fill with eggs immediately after involution of ovary (c.150th).

Discussion: Progamotaenia diaphana was redescribed very briefly by Beveridge (1976) based on a single specimen assumed to be type material and a small number of fragmented specimens from a captive wombat. Although the latter collection suggested that *Lasiorhinus latifrons* might be the usual host of *P. diaphana*, no material had been seen from free-living hosts, and the very closely related cestode, *P. festiva*, had been collected from the bile ducts of free-living *Vombatus ursinus* (Beveridge 1976). Subsequently, collections of cestodes from *L. latifrons* in South Australia were tentatively identified as *P. festiva* (Rudolphi 1819) as they did not conform exactly to the description of *P. diaphana*, and doubt was thrown on the status of *P. diaphana* itself (Presidente & Beveridge 1978). Abundant collections now to hand indicate that *P. diaphana* is a distinctive form, probably warranting specific status, and that doubt as to the identity of Presidente & Beveridge's material was due to a lack of appreciation of the extent of variability in the species.

The present redescription differs from that of Beveridge (1976) in a number of points. A prominent external seminal vesicle was present in the new material, but was stated as being absent in the earlier description. The number of testes per group was previously reported as 17–21, but in the new material is 18–33 per group or 39–63 per proglottis. Part of this variability is due simply to variation between individual cestodes. In two strobilae examined, the range and mean number of testes per proglottis based on examination of 10 proglottides in each strobila was 52–63 (56) and 39–53 (46). Number of testes per proglottis in the related *P. festiva* is 70–130, so that in spite of the variability, testis number is still a useful method of distinguishing the species.

In the type specimen redescribed by Beveridge (1976) early insemination of proglottides was followed by vaginal atrophy. This phenomenon was not recorded in the orginal description (Zschokke 1907) and was not present in the other material described by Beveridge

Figs 24-29. *Progamotaenia diaphana* (Zschokke). 24. transverse histological section of lateral region of proglottis showing cirrus sac, uterus and musculature; 25. mature proglottis; 26. mature proglottides showing variation in proglottis shape and testis distribution; 27. gravid proglottis; 28. scolex; 29. mature proglottis showing variation in testis distribution. Scale lines 0.1 mm.

(1976). In the new material, insemination invariably occurs after the male reproductive system of a particular proglottis has started to function and vaginal atrophy never occurs following insemination. The distal vagina is frequently difficult to see in mounted specimens, so fragments of the type material were serially sectioned, showing that the vagina remained intact in post mature proglottides and suggesting that Beveridge's interpretation based on the single whole mount preparation was incorrect. Beveridge's (1976) suggestion that vaginal atrophy could vary within a species should therefore be ignored. The suggestion has also proven incorrect in the case of *P. lagorchestis* and *P. thylogale* (Beveridge & Thompson 1979); species which were initially confused under the one name.

Two diagrams of the egg of *P. diaphana* were given by Beveridge (1976), one showing the pyriform apparatus ending in two horns and the other showing an undivided pyriform apparatus. Both forms are present in the new material but, being unmounted, it is possible to roll the eggs under a coverslip and show that there are indeed two different types and that they are not the same form viewed from different aspects (Beveridge 1976). The undivided form is identical with that found in *P. festiva* and the divided form may merely be a developmental stage (Beveridge 1976), since it occurs in much lower numbers. This form of pyriform apparatus was illustrated by Böhm & Supperer (1958).

The presence of dark pigment in the scolex of *P. diaphana* was first reported by Böhm & Supperer (1958), and is present in the single scolex among the type material as well as in all lots of new material. The pigment, however, is not invariably present and cannot therefore be used as a distinguishing character.

Beveridge (1976) listed a number of features which distinguished *P. diaphana* from the related *P. festiva*. Of these, the presence of proterogyny and vaginal atrophy should be discarded, while the shape of the uterus requires a subjective assessment and is therefore of doubtful value. The two species differ in the frequent presence of dark pigment in the scolex of *P. diaphana* and differences in the number of testes per proglottis, allowing for the considerable variation which occurs in both species. In view of the present redescription, *P. diaphana* probably warrants continued specific rank, and the specimens described under the name *P. festiva* from *L. latifrons* by Presidente & Beveridge (1978) should be renamed *P. diaphana*. However, Beveridge (1976) has pointed to the extensive variation in specimens of *P. festiva* from various host species, and it is evident that a reassessment of this taxon and *P. diaphana* will be necessary when life histories are known and cross infection experiments can be undertaken.

The data presented above establish *L. latifrons* as the usual host for *P. diaphana*. Böhm & Supperer (1958) reported *P. diaphana* from a captive *Vombatus ursinus* in Europe, but subsequent correspondence by a colleague with Supperer established that this animal was in fact *L. latifrons* (Presidente & Beveridge 1978), and had earlier been misidentified. In his original description, Zschokke (1907) gave no details as to how he obtained his specimens, and gave the host name as *Phascolomys wombat*, a name which is now placed as a synonym of *V. ursinus*, but which could have been applied to any of the species of wombats. If, as indicated by data associated with the material considered now to be type material, the species was initially collected by E. Angas Johnston, then *L. latifrons* may be the type host. Angas Johnston was a doctor and amateur naturalist who lived in Adelaide.

Progamotaenia zschokkei (Janicki, 1909)

Material examined: From *Onychogalea fraenata*: 1 specimen, Dingo, Qld, 12.vii.1975, J. E. Nelson; 5 specimens, captive animals originating from Dingo, Qld, March 1978, 19.ii.1979, I. Beveridge; 8 specimens, same data, 26.vii.1979, R. Speare. From *Onychogalea unguifera*: 4 specimens, "Kimberley Ranges", W.A., 31.viii.1976, 6.xii.1976, L. Keller; 2 specimens, Chadshunt Stn, Qld, 6.viii.1979, R. Speare and P. M. Johnson. From *Lagorchestes conspicillatus*: 5 specimens, Inkerman St, Qld, 7.ix.1979, 1.ii.1979, P. M. Johnson; 3 specimens, Mingela, Qld, 10.v.1979, I. Beveridge. From *Thylogale stigmatica*: 10 specimens, El Arish, Qld, 30.vii. 1978, I. Beveridge. From *Petrogale penicillata*: 3 specimens, Hervey's Range, Townsville, Qld, 3.iv.1979, I. Beveridge. From *Macropus agilis*: 5 specimens, Marrakai Plains, N.T., 29.ix.1973, L. Corner; 13 specimens, Townsville, Qld, 15.vi.1978, I. Beveridge.

Discussion: *Onychogalea fraenata*, *O. unguifera* and *Macropus agilis* are new hosts for *Progamotaenia zschokkei*. Part of the material listed above from *M. agilis* was identified erroneously as *P. lagorchestis* by Beveridge

(1976). *M. agilis* is not a host of *P. lagorchestis* or of *P. thylogale*, a species which was confused under the former name by Beveridge (1976). Further specimens of *P. zschokkei* from *Thylogale stigmatica* and *Petrogale penicillata* confirm earlier reports from these hosts based on rather poorly preserved material (Beveridge 1976).

There was considerable size variation in the specimens of *P. zschokkei* examined. Those from *O. fraenata* measured 95–120 x 11–12 mm; specimens from *O. unguifera* were larger, measuring 380–460 x 8–12 mm. Specimens from *L. conspicillatus* were 160–170 mm long and varied from 8–13 mm in width. Cestodes from *M. agilis* were long (130–185 mm) but only 4–6 mm wide while specimens from *P. penicillata* and *T. stigmatica* were the smallest, measuring 58–61 x 2–3 mm and 50–90 x 2–3 mm respectively. In spite of the great difference in size, there were no significant differences in internal morphology. The size difference may be due to the influence of the host, but experimental infections will be needed to demonstrate whether this is the cause of the observed differences, or whether a species complex exists. Similar size variation has been noted in *P. festiva* and *P. macropodis* (Beveridge 1976).

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